



UMEÅ UNIVERSITY

SEASONS OMITTED

Seasonality of Arctic Plant Activity and Nitrogen Uptake Beyond Summer

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Dissertation for PhD

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And Ilúvatar spoke to Ulmo, and said: 'Seest thou not how here in this realm in the Deeps of Time Melkor hath made war upon thy province? He hath bethought him of bitter cold immoderate, and yet hath not destroyed the beauty of thy fountains, nor of thy clear pools. Behold the snow, and the cunning work of frost! Melkor hath devised heats and fire without restraint, and hath not dried up thy desire nor utterly quelled the music of the sea. Behold rather the height and glory of the clouds, and the everchanging mist; and listen to the fall of rain upon the Earth! (...)'

Then Ulmo answered: 'Truly, Water is become now fairer than my heart imagined, neither had my secret thought conceived the snowflake, nor in all my music was contained the falling of the rain. (...)'

The Silmarillion, J.R.R Tolkien

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List of papers

This thesis summarises and comments on three papers, which will be referred to by their Roman numerals throughout.

1. *Arctic plant nitrogen uptake in winter equals summer nitrogen uptake*
Emil Alexander Sherman Andersen, Gesche Blume-Werry,
Chenxin Feng, Friederike Gehrman, Niki Leblans, Anders
Michelsen, Johan Olofsson, Josefine Walz, Ellen Dorrepaal,
Manuscript
2. *Year-round seasonal variation in bryophyte associated nitrogen
fixation in a low arctic ecosystem, Northern Sweden*
Emil Alexander Sherman Andersen, Signe Lett, Anders Michelsen,
Ellen Dorrepaal, Johan Olofsson,
Manuscript
3. *Bryophytes photosynthesize predominantly outside of the summer
season in northern latitudes*
Emil Alexander Sherman Andersen, Signe Lett, Anders Michelsen,
Johan Olofsson, Ellen Dorrepaal, Gesche Blume-Werry,
Manuscript

Author contributions

Paper I:

ED, NL, and JW designed and set up the study. **EASA**, JW, NL, and FG planned and conducted the field and lab work. AM performed analysis of soil-extracted N-isotopes. **EASA**, ED, JO, and CF performed the data analysis. **EASA** drafted the manuscript, and all co-authors (GBW, CF, FG, NL, AM, JO, JW, ED) contributed to the writing, validation of text and analysis, and approved the final version.

Paper II:

EASA, SL, and ED designed the study, **EASA** and SL set it up. **EASA** conducted the fieldwork. AM performed ARA and isotopic analyses. **EASA** and JO performed the data analyses. **EASA** drafted the manuscript and all co-authors (SL, AM, JO, ED) contributed to the writing, validation of text and analyses, and approved the final version.

Paper III:

EASA, SL, and ED designed the study, **EASA** and SL set it up. **EASA** conducted the fieldwork. AM performed acetylene reduction assay and isotopic analyses. **EASA**, JO, and GBW performed the data analyses. **EASA** drafted the manuscript and all co-authors (SL, AM, JO, ED, GBW) contributed to the writing, validation of text and analyses, and approved the final version.

Abbreviations:

EASA: Emil Alexander Sherman Andersen; **ED**: Ellen Dorrepaal; **NL**: Niki Leblans; **JW**: Josefine Walz; **FG**: Friederike Gehrmann; **AM**: Anders Michelsen; **JO**: Johan Olofsson; **CF**: Chenxin Feng; **GBW**: Gesche Blume-Werry; **SL**: Signe Lett

Abstract

In boreal and arctic ecosystems, the seasons experience pronounced temporal variation, leading to high variability in environmental conditions. Plants are challenged by a short (aboveground) growing season during the summer and an extended period of cold temperatures, low light or snow cover during the long winter. Furthermore, nutrients are scarce and highly contested. Plants have evolved a range of mechanisms to survive and grow even in these harsh conditions, and both vascular plants and bryophytes may be able to use the “shoulder seasons” of spring and autumn. Yet, much of the research has focused on the processes during the summer season and less on seasons beyond; the full extent of annual seasonal variation in plant activity remains unexplored.

In this thesis, I explore three aspects of plant seasonal activity in a low arctic ecosystem in Northern Sweden. I traced root potential nitrogen (N) uptake in vascular plants by using isotopic ^{15}N labelling over multiple points throughout the year in the field. Furthermore, I explored two aspects of bryophyte activity in a range of species throughout a year: N_2 -fixation, measured with the acetylene reduction assay, as well as photosynthesis.

My results show that vascular plants can acquire N at any time during the year in equal proportions, and potentially even more efficiently in winter. Bryophytes are less active in the middle of the winter, but activity in both photosynthesis and N_2 -fixation peaks in the shoulder seasons for a majority of species. Interestingly, some species show activity even in the early and late winter. In contrast activity during the summer is much more limited, potentially because of drought, for many bryophyte species.

Overall, winter—a season often omitted from studies in boreal and arctic ecosystems—is as important for plant activity as summer, if not more so given its longer duration. To fully understand plant activity in these high-latitude ecosystems, the winter season has to be considered. The results from the vascular plants show that there is a temporal mismatch in the acquisition of nutrients and carbon, while bryophytes display a continued ability to acquire both nutrients and carbon. This has implications for understanding plant growth and survival in these ecosystems along with carbon and N dynamics. The concepts of growing season and “winter” should shift towards a more nuanced seasonal aspect where activity during the winter season is integrated and considered.

Abbreviations

AR: Acetylene reduction

ARA: Acetylene reduction assay

C: Carbon

C₂H₂: Acetylene

C₂H₄: Ethylene

CO₂: Carbon dioxide

ER: Ecosystem respiration

GPP: Gross primary production

GWC: Gravimetric water content

¹⁵N: Heavy stable isotope of nitrogen

N: Nitrogen

N₂: Dinitrogen

NH₃: Ammonia

NH₄⁺: Ammonium

NO₃⁻: Nitrate

NEE: Net ecosystem exchange

PAR: Photosynthetically active radiation

Vol.: Volume

Introduction

Seasons—winter omitted

“Dry, leafless, (...) trees stood crowded and aisled for miles along these hills, their roots withered in the earth. They were ready (...) to lie under frost and snow for thousands of days and nights, to rot in the long, long thaws of Spring, to enrich with their vast death the earth where (...) their seeds lay buried now.

Patience, patience...”

— *Planet of Exile*, Ursula K. Le Guin —

What is a season? As the Earth circles the sun at a tilted angle along its axis, the incoming solar radiation varies in an annual cycle. This gives rise to seasonality across the planet. From the perspective of a temperate climate in Europe, the year is often divided into four relatively distinct seasons of summer, autumn, winter, and spring. Yet, as we move up towards the higher latitudes, the seasons shift until almost only summer and winter are left, with short shoulder seasons in-between. Summer is a short season with eternal light as the midnight sun takes hold above the polar circle (66°33' 50.2" N). Winter, in contrast, is cold and dark with polar night for days, weeks, or months. Even when there is some direct sunlight after the sun comes back, much of the landscape is covered in snow so that the light does not reach the low-growing plants. The spring and autumn—as traditionally viewed in the temperate regions—are brief periods. This poses a range of challenges for plants growing in these high-latitude regions.

For biological processes, this strong seasonality is important as organisms will have to adapt to the conditions to survive and reproduce (Boyce, 1979; Williams *et al.*, 2015). Yet, we do not have a good description of the seasons at the high latitude boreal and arctic ecosystems, or how to define the gradual changes in meaningful categories (Kelsey *et al.*, 2023; Körner *et al.*, 2023), not even for what is the growing season of plants (but see e.g. Körner *et al.*, 2023). Summer and winter are fairly often described, while spring and autumn have been used by some studies (Bilbrough *et al.*, 2000; Edwards *et al.*, 2006; Larsen *et al.*, 2007b; Miller *et al.*, 2009), sometimes collectively referred to as the shoulder seasons (Larsen *et al.*, 2012; Ernakovich *et al.*, 2014; Blume-Werry *et al.*, 2016). Sometimes a prolonged period of winter known as the cold season (from around September/October or November to May/June) has been used

(Olsson *et al.*, 2003; Schimel *et al.*, 2004; Larsen *et al.*, 2007b). Yet, the importance of spring, autumn, and winter for plant activities as well as the nuances of environmental conditions found during winter, is still overlooked. To understand the seasonality experienced by plants, our temperate view is inadequate and we will have to look elsewhere for inspiration.

The Sámi and other Indigenous people of the northern latitudes define eight seasons based on reindeer herding (Laptander *et al.*, 2024), but the seasons are also relevant for plants in high-latitude ecosystems. I will outline them as they are named by the Sámi of Northern Sweden (the Northern Sámi *Gabna*) and which months they roughly correspond to in Northern Sweden (Figure 1): *Dálvi* is winter of the months January and February, where snow is present and temperatures are cold. During March and April is the spring-winter or *Giddadálvi*, where the sun returns and it starts getting warmer, but there is still snow cover. Spring, *Gidda*, has the beginning of snowmelt in May. Around and after snowmelt is the spring-summer, *Giddageassi*, of June which is the beginning of the summer for many plants as the sun is above the horizon 24 hours a day. Summer, *Geassi*, is the height of the traditional growing season for arctic plants starting after midsummer through July. August is the autumn-summer, *Čakčageassi*, with still warm temperatures, and beginning darkness when plants might fruit and start to senesce. In the autumn months of September and October, *Čakča*, the temperature starts to drop, and deciduous plants lose their leaves with a chance of early snow. Autumn-winter, *Čakčadálvi*, of November and December, has snow and darkness as the polar night arrives with 24 hours without direct sun. These seasons could help explain key differences that are overlooked by only using the four traditional seasons of more temperate climates. For example, spring processes will have to include the nuance of snow-cover with sun (*Giddadálvi*), the beginning of snowmelt with colder soil temperatures (*Gidda*), and after snowmelt with plenty of water availability (*Giddageassi*). Processes in the soil and for plants will be different across these three periods, as I shall explore in the next sections, yet from a traditional perspective of spring-time flowing, the spring might only encompass a few short weeks in May–June.

Others have also tried to define phases of the cold season. Olsson *et al.* (2003) defined five phases of the Alaskan Arctic cold season based on climate, snowpack and activity in the soil. These seasons share some

similarities with the Sámi seasons: *Early Snow*, *Early Cold*, *Deep Cold*, *Late Cold*, and finally *Thaw*. The first two correspond loosely to autumn (*Čakča*) and autumn-winter (*Čakčadálvi*), but vary considerably depending on freezing and snow conditions. *Deep Cold* and *Late Cold* correspond to winter (*Dálvi*) and winter-spring (*Giđđadálvi*) of more stable snow-cover and cold air temperatures. The *Thaw* period matches

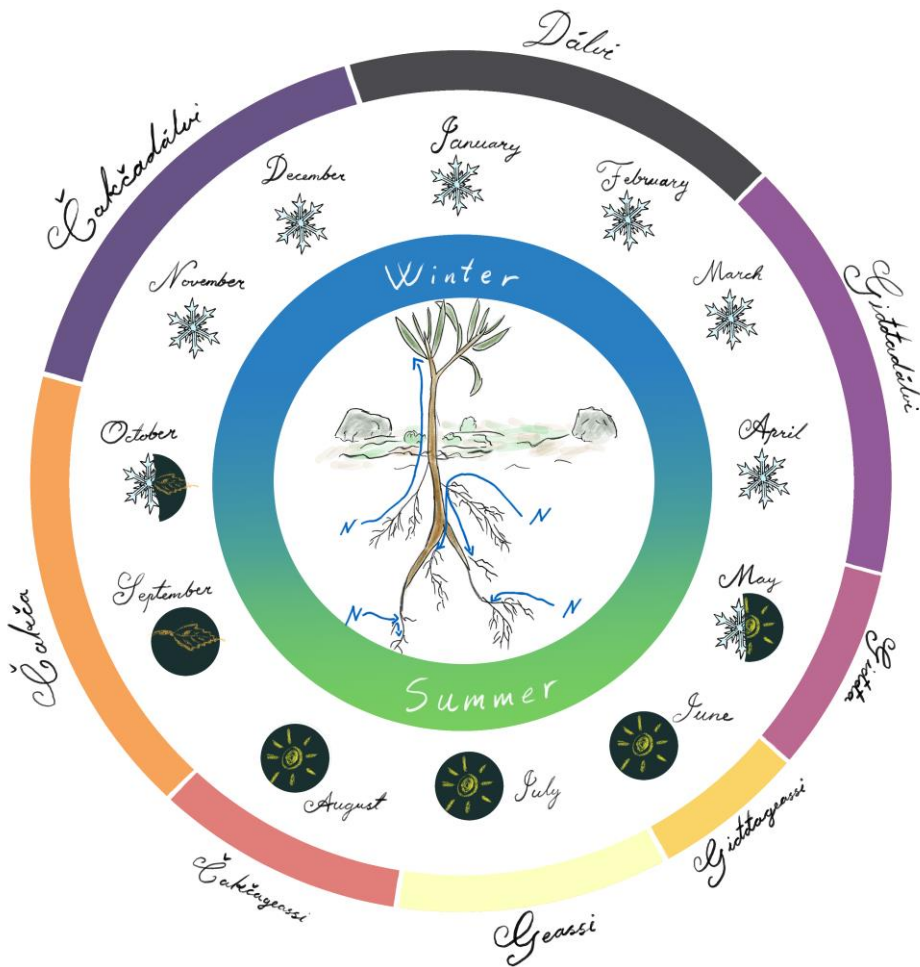


Figure 1 The seasons as seen from different seasonal perspectives in the high latitude site Abisko, Northern Sweden. The seasons are defined over winter and summer, with a long snow-covered period, and brief spring and autumn (each circle corresponding to a month). The Northern Sámi seasons can expand on the understanding of seasons for plant activity, such as nutrient uptake, beyond summer only. Illustration by E.A.S. Andersen

spring (*Gidda*) and spring-summer (*Giddageassi*) with warm temperatures and snowmelt. These seasons are more closely linked to environmental conditions matching the Alaskan Arctic and will not perfectly match low-Arctic or boreal systems where the Sámi seasons might still apply. The seasonality is not static across the latitudes, nor longitude (Lisovski *et al.*, 2017) highlighting the importance of not tying the seasons strictly to months, but defining them flexibly.

Regardless of how the seasons are defined, it is important to keep in mind the variability of the “cold season” or snow-covered season to avoid implying stagnant biological processes of winter over what is an extensive period of time. If we are to understand plants in these high-latitude regions we are required to look past temperate seasonality and, crucially, to look beyond summer alone.

Plants in the Arctic

Calvin: “What motivates an onion?”

Hobbes: “Fame, I suppose.”

— *Calvin and Hobbes*, November 11th 1986, Bill Watterson —

The high latitudes—encompassing arctic, low-arctic, and boreal ecosystems—pose challenging environments for plants to thrive. Plant growth and survival is restricted because of environmental constraints, with low light limiting photosynthesis (Míguez *et al.*, 2015), cold temperatures strongly inhibit water flow, and snow covering the landscape prevents light from reaching the plants below (Woolgrove & Woodin, 1995). Conversely, the snow cover can provide thermal insulation by decoupling the soil and air temperatures, stabilising soil temperatures if the snow is thick enough (Olsson *et al.*, 2003; Mörsdorf *et al.*, 2019) and provide essential moisture during thaw and summer (Billings & Bliss, 1959, Walker *et al.*, 1995; Semenchuk *et al.*, 2016). Furthermore, nutrient availability is low (Shaver & Chapin III, 1980; Nadelhoffer *et al.*, 1992; Wookey *et al.*, 1995; McKane *et al.*, 2002; LeBauer & Treseder, 2008; Zamin & Grogan, 2012; Du *et al.*, 2020), inhibiting growth potential of plants. Nevertheless, plants have adapted to these environments (Billings & Mooney, 1968; Alberdi *et al.*, 2002).

The growing season for plants in these high-latitude ecosystems is strongly linked to the seasonality of the environmental constraints. As described in the previous section, we lack a proper definition of the seasons

in these high latitudes. Instead, the summer has often been the main focus as it is assumed that a majority of plant activity takes place during the summer growing season (June–August) (Billings & Mooney, 1968; Shaver & Chapin III, 1980; Nadelhoffer *et al.*, 1992; Laine *et al.*, 1994; Larsen *et al.*, 2007a; Lloyd *et al.*, 2011). Yet, studies have found that even after leaf senescence, roots continue to grow belowground well into the autumn (*Čakča*) (Iversen *et al.*, 2015; Sloan *et al.*, 2016; Blume-Werry *et al.*, 2016). Furthermore, bryophyte plants might be able to photosynthesize well outside of the summer season (Lösch *et al.*, 1983; Street *et al.*, 2012; Bjerke *et al.*, 2013) as they keep their photosynthetic tissue all year. Despite the duration of the seasons outside of summer, we do not have a comprehensive understanding of plant processes during the whole year in high-latitude ecosystems.

The current understanding of plant processes outside of the summer growing season centres around preparations for the next summer. During autumn (*Čakčageassi* and *Čakča*) plants are expected to reallocate resources (nutrients and carbon (C) from photosynthesis) from shoots to belowground organs (Bret-Harte *et al.*, 2002; Olsrud & Christensen, 2004). Furthermore, the long cold season (stretching from October/November to May/June) requires hardiness against frost, especially for plants growing above the snow (Öquist & Huner, 1991; Adams III *et al.*, 2002). With storage of photosynthetic C from the summer and frost hardiness where necessary the plants are ready for the next (aboveground) growing season.

The effect of snow cover on summer plant processes is multifaceted. Besides providing an insulating layer during the cold months, a deep snow cover can benefit plants and shrubs for the upcoming summer season by increasing nutrient availability (Mörsdorf *et al.*, 2019). Yet, plant phenology and productivity during the summer is dependent on the timing of snowmelt (Billings & Bliss, 1959; Semenchuk *et al.*, 2016) and a deep snow cover and subsequent late snowmelt will also delay leaf bud-break (Sweet *et al.*, 2014). However, despite the snow-covered period seeming like a stagnant period of waiting for plants, this might not be the case.

The cold season might be used by plants more extensively than expected. Even before snowmelt in *Giddadálvi* and *Gidda* some evergreen plants have been found to photosynthesize under the snow (Starr & Oberbauer, 2003; Larsen *et al.*, 2007b). Meanwhile, even though we know belowground growth continues into autumn (Iversen *et al.*, 2015; Sloan *et*

al., 2016; Blume-Werry *et al.*, 2016), we do not know how long the roots continue to be active and take up nutrients. This raises questions about when the plant activity actually starts and if the plants are dormant during the winter. For much of the cold season and especially mid-winter (*Dálvi*) very little research has been done.

For a different group of plants, bryophytes (the non-vascular plants of mosses, hornworts, and liverworts), the environmental constraints are roughly the same, but there are important differences. Bryophytes lack true roots and rely on atmospheric deposition for their water and nutrient uptake (Turetsky, 2003). Besides lacking nutrient-absorbing root systems, they also lack belowground overwintering buds. Instead they have adapted to a wide range of environmental conditions and can often survive strong desiccation (Dilks & Proctor, 1974; Proctor & Tuba, 2002; Turetsky *et al.*, 2012; May *et al.*, 2018), cold temperatures (Harley *et al.*, 1989; Turetsky *et al.*, 2012), and can photosynthesize under low light conditions (Harley *et al.*, 1989; Marschall & Proctor, 2004; Wang *et al.*, 2016) even during winter (Lösch *et al.*, 1983). While they are more tolerant of harsh winter conditions, they also exhibit less control over water loss (Elumeeva *et al.*, 2011). They are thus expected to be sensitive to warm and dry summers (Bengtsson *et al.*, 2016; May *et al.*, 2018). They are remarkably quick at recovery after thawing (Bjerke *et al.*, 2013, Kubásek *et al.*, 2014) and seem to be especially active during the shoulder seasons of spring and autumn (Gunnarsson, 2005; Slate *et al.*, 2024). Yet, again, it is uncertain how active bryophytes are during mid-winter, even if there are reasons to believe they can be active under harsh winter conditions (Lösch *et al.*, 1983; Harley *et al.*, 1989; Moffett, 2015).

For plants—both vascular plants and bryophytes—there is a strong link to the seasonal changes, yet for many aspects of plant activity, there are few studies from outside of the summer growing season (*Giddageassi* to *Geassi/Čakčageassi*). To measure plant activity outside summer different plant processes could be used. Primary production (photosynthesis) is one way, as it directly measures plants' ability to acquire energy in the form of C. For vascular plants, there are a few studies that have measured photosynthesis outside of the summer seasons. Larsen *et al.* (2007b) estimated that 19% of annual CO₂ uptake happens during the cold season based on the months October, November, April, and May. Meanwhile, Starr & Oberbauer (2003) found spring (May, *Gidda*) photosynthesis under the snow for evergreen plants. And Street *et al.* (2012) found that

the primary production of bryophytes in March–May (*Giddadálvi–Gidda*) was much higher than that of vascular plants.

Besides primary production, which is linked to photosynthetic tissue, nutrient acquisition might extend beyond the summer if roots can be active belowground when the soil is partly unfrozen. In a temperate coastal heath in Denmark Andresen & Michelsen (2005) found nitrogen (N) uptake in winter. It might be possible in high-latitude ecosystems to also have nutrient uptake even in winter or during the snow-covered period. While it might be difficult to study plant activity by photosynthesis (except for bryophytes and evergreen plants), nutrient uptake, such as N, could prove a way of measuring activity.

Vitamin N—the importance of nitrogen for plants

“When you wake up in the morning, Pooh,” said Piglet at last, “what’s the first thing you say to yourself?”

“What’s for breakfast?” said Pooh.

— *Winnie-the-Pooh*, A.A. Milne —

Nitrogen (N) is a vital macronutrient for plants, it is a building stone for amino acids and therefore in proteins as well as DNA, chlorophyll and more. N comes in a variety of forms and most plants prefer inorganic N primarily as ammonium (NH_4^+) or nitrate (NO_3^-), where the former is more commonly used (McKane *et al.*, 2002; Reid & Hayes, 2003), but can also use organic N sources from amino acids (Sorensen *et al.*, 2008). The process of taking up N happens through nitrate and ammonium transporters over an electrochemical gradient, meaning it is an active process that costs energy to maintain (Reid & Hayes, 2003; Kiba & Krapp, 2016). N-uptake is furthermore reduced under low temperatures (Laine *et al.*, 1994; Lloyd *et al.*, 2011), which is a major feature of the cold season in high-latitude ecosystems.

In high-latitude regions, N is considered a limiting resource for plant growth (Wookey *et al.*, 1995; McKane *et al.*, 2002; LeBauer & Treseder, 2008; Zamin & Grogan, 2012; Du *et al.*, 2020) and, for example, fertilization with N often result in large increases in plant production and biomass (Zamin *et al.*, 2014; Du *et al.*, 2020). Since N is scarce, plants compete for it both with each other and with soil microbes. To avoid fierce competition, arctic plants have adapted different niches for timing and type of N-uptake depending on competition (McKane *et al.*, 2002).

Though overall limiting, N availability varies seasonally depending on microbial processes of mineralisation and immobilisation. These processes are temperature dependent (Giblin *et al.*, 1991; Hobbie & Chapin, 1996; Mikan *et al.*, 2002; Schimel *et al.*, 2004; Brooks *et al.*, 2011) and will change during the year. High mineralisation has been reported during winter and spring before snow melt-out (Brooks *et al.*, 1996; Hobbie & Chapin, 1996; Grogan & Jonasson, 2003; Schimel *et al.*, 2004; Kielland *et al.*, 2006) when NH_4^+ and organic N is released from microbial dieback (Lipson *et al.*, 1999; Grogan & Jonasson, 2003; Schmidt & Lipson, 2004; Grogan *et al.*, 2004; Edwards *et al.*, 2006; Schimel *et al.*, 2007; Buckeridge & Grogan, 2010). Over summer, the concentration of available N is expected to decrease as it gets bound in the growth of both plants and microorganisms (Lipson *et al.*, 1999; Andresen & Michelsen, 2005). Soil N concentrations are then expected to increase again when aboveground plant activity ceases into autumn (Mörsdorf *et al.*, 2019).

These seasonal process leads to relatively high N availability during winter, and low availability but high demand during summer. Furthermore, many vascular plants lose their photosynthesizing tissue during the cold season, and even the ones that retain their leaves might experience inhibited activity (Öquist & Huner, 2003; Míguez *et al.*, 2015) and have long recovery times when photosynthesis cannot be active although environmental conditions allow it (Ottander *et al.*, 1995; Saarinen *et al.*, 2011). The (vascular) plants are therefore limited to the short aboveground growing season when they can acquire C to power the N-uptake. The combination of a short period of energy supply and low N-availability seemingly limit plant N-acquisition to a highly competitive summer. However, the observed N-consumption does not match the availability during the growing season (Bilbrough *et al.*, 2000; Grogan & Jonasson, 2003; Miller *et al.*, 2009; Edwards & Jefferies, 2010; Larsen *et al.*, 2012; Riley *et al.*, 2021). What is left to assume is that N-use and N-uptake do not necessarily need to occur near simultaneously. Winter microbial activity has been found in several studies (Brooks *et al.*, 1996; Schimel *et al.*, 2004; Larsen *et al.*, 2007a; McMahon *et al.*, 2009). Similarly, plant N uptake has been found quite late in the year (October/November) (Larsen *et al.*, 2012; Blume-Werry *et al.*, 2019). Thus, there are reasons to believe that N-uptake during winter is important for plants, especially if combined with potentially mild subnivean conditions (Olsson *et al.*, 2003; Mörsdorf *et al.*, 2019). This would lead to a strong temporal mismatch in nutrient and energy acquisition as plants use energy during the long cold

season to acquire nutrients, while the nutrients are used for more energy (C) capture (and growth) during the growing season.

While vascular plants rely on their root system to take up N, bryophytes have developed another method to acquire N. In bryophytes, a group of microorganisms, collectively called diazotrophs, live on or in the bryophytes and are the ones responsible for the fixation of atmospheric N₂. They include a wide variety of species, from cyanobacteria (Sprent, 2005; Jean *et al.*, 2020; Holland-Moritz *et al.*, 2021) over methanotrophs and Actinobacteria (Bragina *et al.*, 2012; Vile *et al.*, 2014) and several other taxa (Jean *et al.*, 2020; Holland-Moritz *et al.*, 2021). Being able to fix N₂ from the atmosphere means organisms have, in principle, access to unlimited N (approx. 78% dry vol. of the atmosphere is N₂). The process of N₂-fixation is done by a family of enzymes (nitrogenases) that reduce the inert N₂ from the atmosphere and produce ammonia (NH₃) (Eady, 1996; Hoffman *et al.*, 2014) used by the organisms. The downside is that N₂-fixation is an energy-demanding process (Eady, 1996; Turetsky, 2003; Bellenger *et al.*, 2020). Nonetheless, it can contribute a substantial proportion of the annual N input to high-latitude ecosystems (DeLuca *et al.*, 2002; Larmola *et al.*, 2014).

The process of N₂-fixation is limited by environmental conditions that change over the seasons, such as moisture, temperature, and light availability. Of those, moisture is probably the most limiting factor for N₂-fixation associated with bryophytes (Smith, 1984; Belnap *et al.*, 2001; Gundale *et al.*, 2009, 2012; Stewart *et al.*, 2014; Lett & Michelsen, 2014; Rousk & Rousk, 2020; Alvarenga & Rousk, 2022) as bryophytes cannot control their water gain and loss the way vascular plants can (Proctor & Tuba, 2002; Kappen & Valladares, 2007; Elumeeva *et al.*, 2011). Moisture limitation will limit bryophyte N₂-fixation during dry summers (Gundale *et al.*, 2009, 2012; Stewart *et al.*, 2014; Rousk *et al.*, 2014), but they might not have the same problem during the cold seasons since some bryophytes have been observed using ice-nucleation to gain water (Moffert, 2015). While temperature might also be limiting N₂-fixation, it is unclear what the optimal temperature for bryophyte-associated N₂-fixation is. Some studies have suggested as high as 20 °C (Smith, 1984; Chapin *et al.*, 1991; Houlton *et al.*, 2008), while others suggest down to 14 °C (Rousk *et al.*, 2018). However, the surface temperature of the bryophytes can be much higher than the air temperature (Kanda, 1986; Perera-Castro *et al.*, 2020), which is typically measured in studies such as mentioned above. As

temperature is linked to water availability, the effect might be more determined by adequate moisture (Stewart *et al.*, 2011, Lett & Michelsen, 2014; Rousk & Rousk, 2020). High light intensities do not seem to be required since bryophyte N₂-fixation can reach optimal conditions well below summer light intensities (Zielke *et al.*, 2002). This might be linked to their ability to photosynthesis under low light (Harley *et al.*, 1989; Marschall & Proctor, 2004; Wang *et al.*, 2016), which enables them to supply the energy needed for N₂-fixation. Taken together, these factors suggest that bryophyte-associated N₂-fixation may very well be present outside of summer, and indeed in several studies, the shoulder seasons have been found highly important for rates of N₂-fixation, but species-dependent (DeLuca *et al.*, 2002; Zackrisson *et al.*, 2004; Lett & Michelsen, 2014; Lett *et al.*, 2024) and it could be that bryophytes are even able to fix N₂ during the deep cold of winter (Dálvi).

Since N is an essential and limiting resource for plants in high-latitude regions N-uptake is a good indicator of plant activity. This goes both for vascular plants, where belowground roots can potentially continue being active, as well as opportunistic bryophytes that can acquire atmospheric N along with their potentially continuous photosynthesis.

Aims and Objectives

Studies of plant activity in high-latitude regions have been limited to the summer growing season, yet a growing body of literature is suggesting that the cold season with its various phases could be as important. Although how to define the seasons in the ecosystems of the boreal and Arctic is and will remain unanswered here, some aspects of the seasonality will be explored in this thesis. Especially the plant activity outside of the summer growing season, which—with its long duration—can contribute substantially to plant processes.

This thesis attempts to explore if and when plants are active during the year in a high latitude (low arctic) ecosystem, to gain an understanding of year-round plant processes with a special focus on the nitrogen dynamics in vascular plants and bryophytes. With this lofty goal as a foundation, the work of this thesis' three chapters aims to explore:

- I) The year-round potential for nitrogen uptake in vascular plants in a high latitude tundra heath ecosystem.
- II) Seasonal nitrogen fixation by bryophytes across a wide range of species to reveal when N₂-fixation is most prevalent throughout the year.
- III) Photosynthetic activity of bryophytes throughout the year in a wide range of species.

Methodology

“If [a scientist] sees a thing, he must say that he sees it, whether it was what he thought he was going to see or not. See first, think later, then test. But always see first. Otherwise you will only see what you were expecting.”

— *So long, and Thanks for all the Fish*, Douglas Adams —

To uncover the seasonal changes in different plants, two experiments were set up at or near the Abisko Scientific Research Station (ANS, 68°21'N, 18°49'E) in the Torneträsk region (Fig. 2) approx. 200 km north of the polar circle in a low-arctic ecosystem. For Paper **I**, two locations along a strong precipitation gradient were selected and sampling was done at each location. One location was close to ANS (c. 405 m a.s.l), while the other location (c. 610 m a.s.l) was close to Vassijaure station (68°25'N, 18°15'E). The precipitation varied from 347 mm at ANS to 859 mm at Vassijaure (SMHI 1991–2020), while temperature varied from an annual mean of 0.3 °C (ANS) to –0.5 °C (Vassijaure). For Papers **II** and **III**, bryophyte species were collected from around the Torneträsk region and transplanted to the scientific nature reserve at ANS (Fig. 2).

Seasonal uptake of nitrogen in vascular plants (WinterEcology)

For Paper **I**, a large-scale field experiment was established with the aim of investigating whether plants continuously take up nitrogen (N) throughout the year, or at the very least, have the potential for belowground activity. Two locations were selected to reflect different precipitation regimes, allowing for an assessment of the impact of varying snow cover. The study spanned 15 measuring periods, roughly once a month, from July 2019 to August 2020.

At each location, we used isotopically labelled ammonium-nitrate ($^{15}\text{NH}_4^{15}\text{NO}_3$, 98 atom%) to trace N-uptake by plants. ^{15}N occurs naturally in the environment, but in trace amounts which makes it excellent for following the path of N in ecosystems by enrichment (Fry, 2006). Each month we applied a small amount (19 mL solution of 1.9 mM or approx. 1.084 mg ^{15}N patch⁻¹) of our ^{15}N -label solution, equivalent to between 111.46 and 136.67 mg N m⁻² (for winter and summer respectively), directly into the soil in five patches at each location (Fig. 3). Three weeks later we returned and harvested the patch (78.5 cm² in summer and 95.0 cm² in winter) which should give sufficient time to detect uptake

(Andresen *et al.*, 2008). The corer used during winter was a sturdier metal corer to get through the frozen soil, while the summer corer was a PVC pipe with metal teeth attached, hence the difference between winter and summer sampling. The teeth made it easier to cut roots but would have made the corer more prone to breaking in frozen soil, so the winter metal corer was simply fitted with a sharpened edge.

For samples of natural ^{15}N abundance, we collected unlabelled samples twice (September 2019 and March 2020). We assumed that the variation in the natural abundance ^{15}N would be minuscule compared to enriched patches, based on Larsen *et al.* (2012).

We then proceeded to separate the plants into aboveground and belowground parts to trace where in the plant the ^{15}N would end up. Furthermore, we looked at extractable ^{15}N from soil and soil microbes to understand where plant-available N would be found in the system. Each

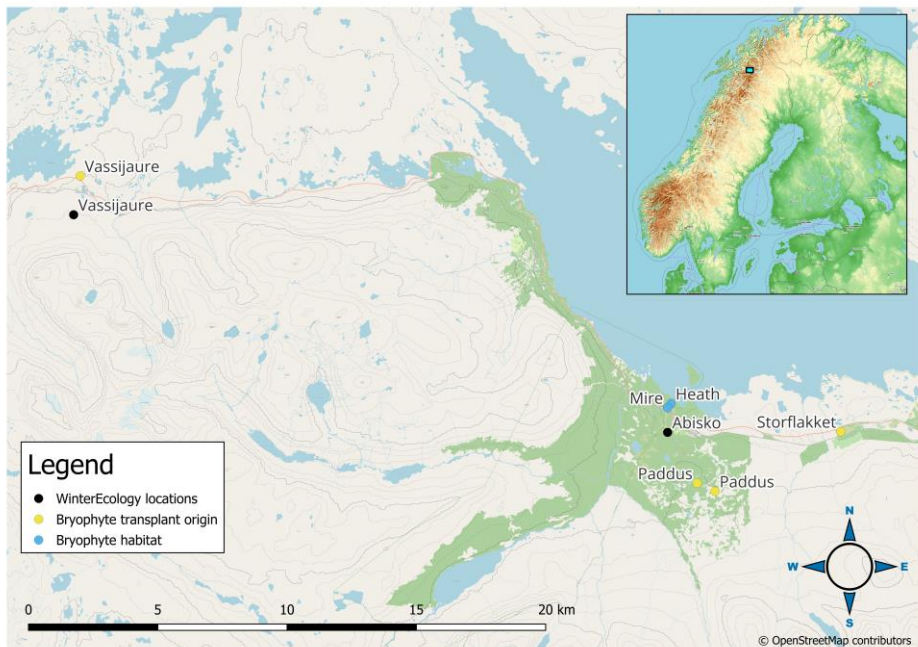


Figure 2 Map of the thesis projects around the Torneträsk Lake, Northern Sweden. The locations of field sites for Paper I (WinterEcology, black) and transplant origin (yellow) and transplanted habitat (blue) of bryophytes from Papers II and III. Created in QGIS. Map-data: © OpenStreetMap contributors and © OpenTopoMap.

of these samples were analysed for isotopic ^{15}N and recovery of the injected ^{15}N was calculated. The combined recovery of each part (plant + soil + microbial) was set as total recovery for relative comparison between seasons.

To account for variation in N found in the soil, we estimated natural N concentrations at injection. As there can be strong seasonal variation in soil N (Cheng *et al.*, 1998; McLaren *et al.*, 2018), we had to account for how much natural N was taken up alongside our added labelled ^{15}N (^{14}N per ^{15}N). The estimation was done with simple linear interpolation from one harvest point to another.

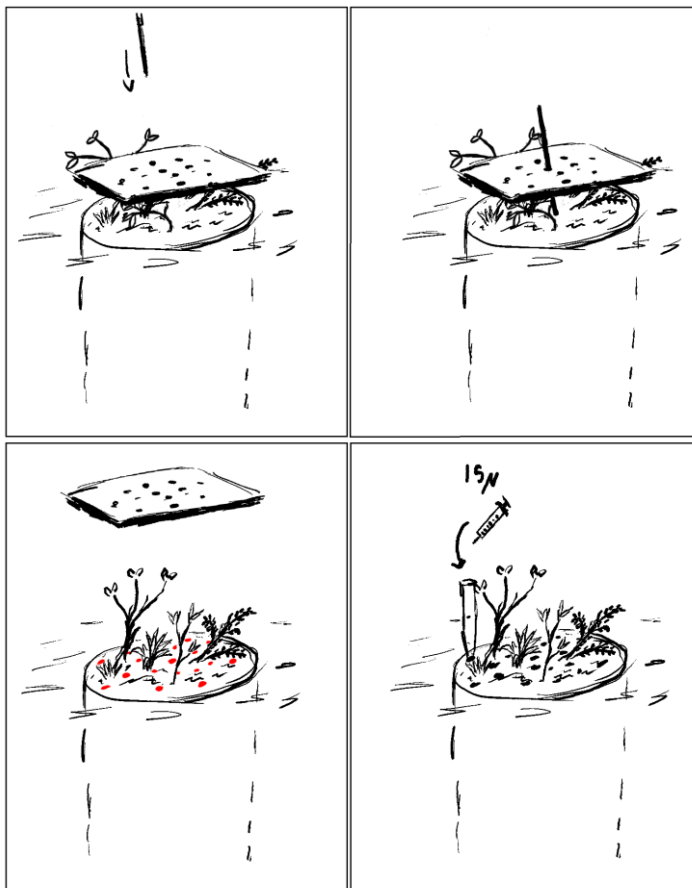


Figure 3 Injection of ^{15}N label. First, 19 holes were made in the soil, before 1 mL of ^{15}N -label was added to each for a total load of 19 mL. Illustration by E.A.S. Andersen

Bryophyte yearly activity

For Papers II and III, we established a common garden experiment within the nature reserve of ANS. As bryophytes do not have roots and do not lose photosynthetic tissue during winter, we measured their activity in a different way than with the vascular plants in Paper I. To understand year-round activity in bryophytes we instead set up an experiment in two parts, to measure different aspects of bryophyte activity: N₂-fixation and photosynthesis.

Nine bryophyte species (from different functional groups as classified by Lett *et al.*, 2022) and one bryophyte species mixture were collected and transplanted to two habitats, mire and heathland, at ANS in the summer of 2020. The selected species were *Aulacomnium turgidum* (Wahlenb.) Schwägr, *Dicranum scoparium* Hedw., *Hylocomium splendens* (Hedw.) Schimp., *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Polytrichum commune* Hedw., *Ptilidium ciliare* (L.) Hampe, *Racomitrium lanuginosum* (Hedw.) Brid, *Sphagnum fuscum* (Schimp.) H. Klinggr., *Sphagnum majus* (Russow) C.E.O. Jensen, and a *Sphagnum* mixture (incl. *S. balticum* (Russow) C.E.O. Jensen, *S. flexuosum* Dozy & Molk., and *S. majus*). Initial identification assumed single species transplants, but upon further verification, one of the *Sphagnum* transplants was found to be a mixture of three *Sphagnum* species. The three *Sphagnum* taxa were transplanted to a mire because of their higher moisture requirements, while the other seven species were relocated to a nearby dryer heathland. Here, *R. lanuginosum* was planted slightly drier than the other heathland transplants to mimic the bare rock habitat it was collected from. Each transplant was a core of 20 cm diameter and down to a max of 30 cm depth (*Sphagnum* spp.), but in most cases 5–15 cm. After transplantation, the species were given 1–3 months to settle. The *Sphagnum* transplants were transplanted last as initial transplants did not survive. For all transplants, untargeted species (vascular and bryophyte) were removed to the best of our abilities. This was repeated the following summer to remove regrowth and ingrowth from the surrounding ecosystem. The first measurement and sampling began in September 2020, with the final session conducted in November 2021. Shoot density was measured in the summer of 2022, the summer after the end of the experiment.

Environmental factors were measured at both habitats. One air temperature sensor—approx. 10 cm—and one PAR (photosynthetically active radiation) sensor—approx. 3–4 cm above ground level—was

installed at each habitat. Soil temperature and moisture were measured in each block (five in total) at 5 cm depth. All measurements were logged every hour. These measurements were used to determine environmental drivers for the bryophyte species' activity.

Bryophyte N₂-fixation

As in Paper I, one measure of bryophyte activity involved monitoring N uptake. However, in bryophytes, N acquisition is highly linked to N₂-fixation from associated diazotrophs. Therefore, in Paper II we focused on the bryophyte-associated N₂-fixation as a measure of nutrient uptake in a year-round experiment.

We used the acetylene reduction assay (ARA)—which measures the reduction of acetylene (C₂H₂) to ethylene (C₂H₄)—to study the N₂-fixation. This process is similar to N₂-fixation as it uses the same nitrogenase enzyme (Hardy *et al.*, 1968; Bellenger *et al.*, 2020). The nitrogenase enzyme is a versatile reductase (Hardy *et al.*, 1968) and can also reduce the triple bond of C₂H₂ to a double bond (C₂H₄). The advantage of this method is its non-destructive nature, as both acetylene and ethylene are gases that can be measured by gas chromatography. Labelling with ¹⁵N₂ would require the destructive harvest of the bryophyte before analysis.

We measured acetylene reduction (AR) with a custom-made cylindrical transparent acryl chamber with a volume of 785 mL (10 cm diameter, 10 cm height), pressed into the bryophyte transplant approx. 3 cm giving a headspace volume of approx. 550 mL. We then exchanged 60 mL of the chamber volume with acetylene gas (≥ 99.6%) (Fig. 4). Samples of 6 mL were taken at 0, 30, and 60 min or for the first three rounds at 0, 60, and 120 min. All samples were then analysed for acetylene and ethylene concentrations. From the change in ethylene concentrations, we could calculate the production and estimate nitrogenase activity. We corrected for potential loss of ethylene by calculating the acetylene lost which could not be accounted for by the ethylene produced.

To further check for leakage and ensure the validity of the results, we also sampled bryophytes from outside the core measurement area of the chamber. The samples were placed in tight vials (20 mL) and 2 mL of the headspace was replaced with acetylene. The vials were left for 24 hours outside at ambient conditions before 6 mL samples were collected.

Afterwards, the samples were aired out and the process was repeated, but the samples were left in a climate chamber at 5 °C and constant light (200–300 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The samples were dried to determine gravimetric water content (GWC). The vial sampling was only repeated three times over the measuring period, corresponding to late winter (March), spring (April) and summer (July). In the summer of 2021, we incubated the last vial with 2 mL dual-labelled $^{15}\text{N}_2$ (98 atom%) after incubating with acetylene.

Bryophyte photosynthesis

Another way of measuring bryophyte activity is to measure their photosynthesis. In Paper III we measured CO_2 -fluxes from the bryophytes, during the same measuring periods as in Paper II, but in the days just prior to measuring the ARA.

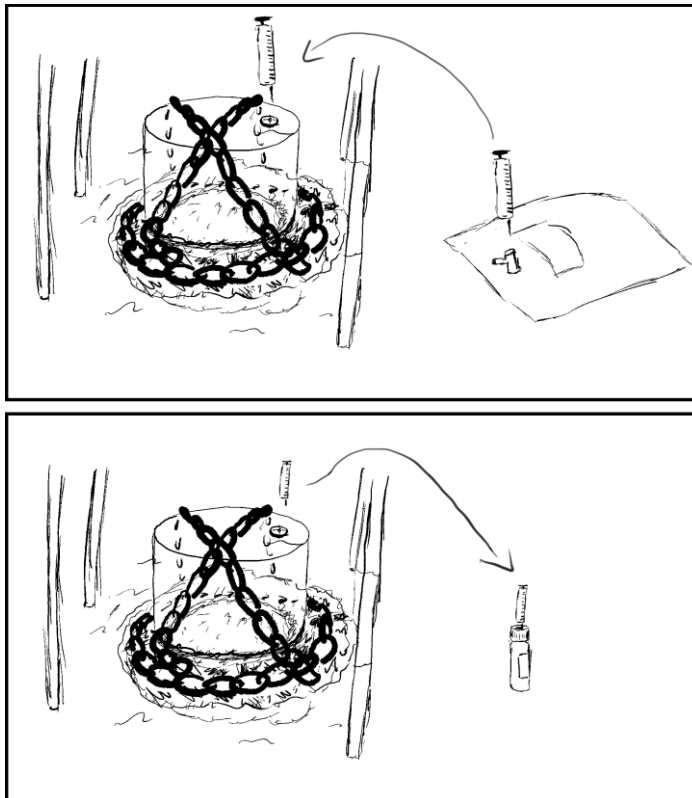


Figure 4 ARA procedure; approx. 10 vol% of the chamber overhead was replaced with acetylene (top). After a set time of incubation (0, 30, and 60 min) a sample was collected (bottom). Illustration by E.A.S. Andersen

We measured CO₂-flux using a portable IRGA and two custom-made acrylic chambers of similar size to the chamber used for ARA measurements in Paper II (Fig. 5). One chamber was kept transparent, while the other chamber was covered with a double-layered plastic bag to measure respiration (dark measurements). Measurements were on the same spots of the bryophyte transplant as in Paper II. We measured over 2 min intervals in summer and 5–10 min intervals in winter to ensure enough build-up of CO₂ to calculate exchange. From the transparent chamber, we measured net ecosystem exchange (NEE) and from the dark chamber, we measured ecosystem respiration (ER). The photosynthesis or gross primary production (GPP) was calculated as the difference between NEE and ER (GPP = NEE – ER). As we had removed other photosynthesizing plants, except for the target bryophytes, we assumed all photosynthesis originated from our target species.

Data analysis

All analyses were performed in R v. 4.2.3 (R Core Team, 2023) and code is available at GitHub for each respective paper.

Papers I and III were analysed with linear mixed-effects models (LMEs) using the package *nlme* (Pinheiro *et al.*, 2023) as well as an ANOVA from the *car* package (Fox & Weisberg, 2019). Paper II was analysed with the package *glmmTMB* (Brooks *et al.*, 2017) as well as the *car* package. The *glmmTMB* function accounts for zero-inflated data from the below detection values of ethylene production.

For Paper I the effect of location (snow regime) and seasonality (measuring period) and interaction was investigated for all recovery fractions and total recovery. A priori contrasts were defined to reduce the complexity of measuring 15 months. The contrasts divided snow-covered and snow-free periods and within each the warm and cold periods.

In Papers II and III seasonality (measuring month) was analysed and if significant environmental drivers were factored with species, but without interaction between drivers in Paper II. A similar procedure was run for vials from Paper II, both vials left in the field and in the climate chamber. The environmental drivers were fewer—for field vials only PAR and bryophyte water content and for vials in the climate chamber only water content.



Figure 5 Bryophyte plots. The ARA (top) and photosynthesis (bottom) used the same spot within the bryophyte transplant. The pictures are representative of the concept but are not the same plot or species. Pictures by E.A.S. Andersen

Results & discussion

“Scientific truth is always paradox, if judged by everyday experience, which catches only the delusive appearance of things.”

— *Value, Price and Profit*, Karl Marx —

From my studies, I have found that plants are active throughout the year in acquiring nutrients (**I**, **II**) and with the potential for photosynthesizing among bryophytes (**III**). Plants show a remarkable capacity to take up nitrogen (N) all year round (**I**), while bryophyte-associated N₂-fixation also extends far beyond the summer season (**II**). Bryophytes also have the ability to continue photosynthesizing well beyond the traditional vascular growth season (**III**). Yet, both photosynthesis and N₂-fixation might be limited by drought during summer. These processes are driven by environmental factors that can vary from year to year.

Vascular plants and winter nutrients

It might be intuitive to believe that plants are dormant during winter when they are covered by snow and the air temperature falls below $-10\text{ }^{\circ}\text{C}$. Paper **I** reveal that this is not the case. Throughout the year plants took up N injected into the soil and the uptake in winter was as efficient as, if not more so, than in summer (Fig. 6). The results strengthen previous studies which presumed that the cold winter season is crucial for plant N requirements (Grogan & Jonasson, 2003; Andresen & Michelsen, 2005; Larsen *et al.*, 2012; Riley *et al.*, 2021). Only a few studies have looked at the midst of the winter (*Dálvi*) during the snow-covered season, but it should not come as much of a surprise that plants can be active outside of what is the traditional aboveground growing season. As N-uptake has been found in plants late into autumn (Larsen *et al.*, 2012; Blume-Werry *et al.*, 2019), as well as during snowmelt (Bilbrough *et al.*, 2000; Grogan & Jonasson, 2003; Grogan *et al.*, 2004; Miller *et al.*, 2009; Edwards & Jefferies, 2010). Yet, while it has been suggested that the N only becomes available to plants during snowmelt (Grogan & Jonasson, 2003), Paper **I** shows that if inorganic N is available during winter, plants can utilize it. Microbes are known to immobilize N during winter (Brooks *et al.*, 1996, 1999; Buckeridge & Grogan, 2010), and indeed most of the labelled ¹⁵N was found in microbes, but this does not mean plants are inactive. Plants consistently had acquisition of ¹⁵N throughout the year. Whether soils have enough plant available N during winter is more uncertain, and could

depend on location, but from estimations in Paper I N would be far more available during winter, than during summer.

Allocation of N within the plants was primarily found in the roots throughout the year, but a surprising proportion was found in aboveground parts (incl. branches of shrubs) during the late spring-winter (*Giddadálvi* and *Gidda*). This could suggest allocation of nutrients in preparation for aboveground summer growth. Yet, even during the deep cold of winter (*Dálvi*) a large fraction of newly taken-up N is found in aboveground plant parts. While some evergreen plants keep N in aboveground leaves during the cold season (Chapin III & Kedrowski, 1983; Larsen *et al.*, 2012), active mid-winter uptake is more surprising. The high aboveground fraction of N may be driven by the high abundance of evergreen species, or shrubs in general, in our study system. Nonetheless, the dynamic of nutrient storage during the cold season might be more complex than previously assumed.

A critical point from Paper I is that the nutrient uptake during the snow-covered season is decoupled from the carbon input. Even evergreen plants, that have their leaves' photosynthetic apparatus inhibited (Öquist & Huner, 2003; Míguez *et al.*, 2015), were found to acquire N. Nutrient uptake and energy supply (in the form of carbon) do not occur simultaneously, but exhibit a strong temporal mismatch. Carbon is absorbed during the light-rich period of the year following snowmelt (*Dálvi* and *Giddageassi*) through to late summer (*Čakčageassi*). This C is stored and later used to acquire nutrients during the dark, and snow-covered period, which in turn supports renewed C capture in the following light period.

Importantly, the insulating effect of snow had an impact on the results of Paper I. Throughout the experiment diel soil temperatures never fell much below freezing, while air temperatures fluctuated around $-10\text{ }^{\circ}\text{C}$ and dropped below $-15\text{ }^{\circ}\text{C}$, showing strong decoupling of air and soil temperature at both locations (Abisko and Vassijaure). Other studies have also found that under sufficient snow cover microbes can be active (Brooks *et al.*, 1996; Schimel *et al.*, 2004; McMahon *et al.*, 2009) and mineralisation may be substantial (Brooks *et al.*, 1996; Hobbie & Chapin, 1996; Grogan & Jonasson, 2003; Schimel *et al.*, 2004; Kielland *et al.*, 2006). Yet, the soil temperature will depend on the onset of snow, which during this first experiment happened around the end of October, before soil temperatures had dropped considerably. In contrast, for Papers II and III snow onset was in the beginning of November and soil temperatures

fell below $-5\text{ }^{\circ}\text{C}$, while air temperatures fell below $-20\text{ }^{\circ}\text{C}$ several times. This should emphasise the importance of snow and cold or mild winter temperatures in cold-season processes for plants.

Bryophyte activity

Except for the mid-winter (*Dálvi*), bryophyte-associated N_2 -fixation (II) was active throughout the year for many species (Fig. 7). This aligns with previous studies that also found that shoulder seasons (spring and autumn) are as important as summer for N_2 -fixation rates (DeLuca *et al.*, 2002; Lett & Michelsen, 2014; Lett *et al.*, 2024), but also expands this to early (*Čakčadálvi*) and late winter (*Giddadálvi*). In our study, the different bryophyte species had some variation in their seasonality of N_2 -fixation, and this was related to the functional type of the species. The *Sphagnum* taxa all had the highest N_2 -fixation during summer (*Geassi*), while the other species had their highest fixation in spring and autumn. Some species started to have high fixation already during the March spring-winter: Polytrichales (*P. commune*) and leafy liverwort (*P. ciliare*). In May, two additional species had high rates: unbranched turf moss (*A. turgidum*) and large cushion moss (*R. lanuginosum*). In spring-summer and summer the wet mosses (*H. splendens* and *P. schreberi*) had strong peaks. During autumn a second peak in N fixation was recorded for all species but the *Sphagnum* and the leafy liverwort. Even the tall unbranched turf moss (*D. scoparium*), which did not have a spring peak, had an autumn and early-winter peak. In other words, several very different species of different functional groups peaked outside the summer season in the so-called shoulder seasons, but also into the winter.

A similar pattern of high spring N_2 -fixation peak for all non-*Sphagnum* species was also found in our vial samples incubated in the field supporting the conclusion of shoulder season importance. Interestingly, the same samples incubated in the climate chamber showed high late-winter (*Giddadálvi*), low spring (*Gidda*), and no measurable summer (*Geassi*) N_2 -fixation (AR) for all non-*Sphagnum* species. A possible explanation for this is that the diazotrophs from the field had a hard time adapting to $5\text{ }^{\circ}\text{C}$ in the climate chambers when moved from high outside temperatures (Chapin *et al.*, 1991; Rousk *et al.*, 2018). Despite this, the summer $^{15}\text{N}_2$ -fixation in climate chambers did show N_2 -fixation in all bryophytes, suggesting that N_2 -fixation, as measured with AR, was below the detection limit but present.

As summer AR values for samples incubated in climate chambers were so low in the non-*Sphagnum* species, the measured AR could not be converted to N₂-fixed in this study. For the *Sphagnum* species, it was possible to calculate an AR:N₂-fixed ratio, which for this study was found to be 0.17:1. This is well below the commonly expected conversion ratio of around 3.2:1 (Hardy *et al.*, 1968), but matches a few other studies of *Sphagnum* (Stewart *et al.*, 2011; Saiz *et al.*, 2019). Still, the ratios are expected to differ across species, which makes comparison of process rates between species difficult, but the seasonal patterns in N₂-fixation activity should still be robust.

The bryophyte-associated N₂-fixation is an energy-demanding process (Turetsky, 2003), and bryophytes lack similar storage organs as vascular plants for storing carbon. As such N₂-fixation could reasonably be assumed to be limited during the dark cold-season. However, unlike vascular plants, bryophytes have quick recovery of photosynthesis when conditions become favourable (Kappen, 1993; Bjerke *et al.*, 2013).

For the photosynthetic activity of the bryophytes (III), a similar pattern emerged as for the N₂-fixation. The majority of species exhibit high GPP outside of the summer season, with many plateauing after a spring increase and then peaking in autumn (Fig. 8). Interestingly, autumn was consistently the period of highest photosynthetic activity across most species. The main exceptions were the three *Sphagnum* species and *P. commune*, all of which peaked in the summer months.

The high summer photosynthetic peaks (III) of the three *Sphagnum* species match other studies that found *Sphagnum* GPP benefitted from higher temperatures when not constrained by water limitations (Deane-Coe *et al.*, 2015; Bengtsson *et al.*, 2021). It also links to the high summer N₂-fixation found in this study (II) and others for *Sphagnum* (Stewart *et al.*, 2011; Rousk *et al.*, 2015; Lett *et al.*, 2024). We do not know if the different seasonality, with a distinct summer peak, depends on species or habitat traits. Since the three *Sphagnum* taxa were transplanted to a mire they might not have been water limited during the summer, and have been better able to utilise the high summer temperatures for photosynthesis (Gunnarsson, 2005; Deane-Coe *et al.*, 2015) and subsequently for N₂-fixation (Rousk, 2022), while the other species might be more constrained by moisture leading to autumn peaks of photosynthesis and N₂-fixation (Rousk *et al.*, 2014). Polytrichales like *P. commune* have, in contrast to most other bryophytes, water-conducting tissue that resembles

that of vascular plants (Héban, 1977; Proctor *et al.*, 1998; Proctor, 2008). This might make them more drought-resistant and explain why they were less water-constrained in their photosynthesis during summer than some other bryophyte species.

For both N₂-fixation and photosynthesis environmental conditions limit the processes. The N₂-fixation (II) was found to be driven by several environmental factors that differed between species. A range of environmental conditions are known to constrain N₂-fixation interactively (Rousk *et al.*, 2017; Rousk, 2022) and not always with a clear linear relationship. Overall moisture was one of the main limiting factors for N₂-fixation associated with bryophytes, which is also in line with other studies (Smith, 1984; Gundale *et al.*, 2009, 2012; Stewart *et al.*, 2014). Bryophytes exhibited limited N₂-fixation below a certain water content threshold, but beyond this threshold, further increases in water content had minimal impact. Besides moisture, temperature was the main limiting factor matching other studies (Stewart *et al.*, 2011; Lett & Michelsen, 2014). Yet, for some species temperature did not have a clear linear relationship with N₂-fixation.

Ultimately bryophyte associated N₂-fixation (II) might be severely limited in summer or during drought periods as would photosynthetic activity (Bengtsson *et al.*, 2016; May *et al.*, 2018)—excluding the seeming drought of winter, as they might be able to use the snow to gain moisture (Moffett, 2015). But photosynthetic activity (III) might be less limited by a single environmental factor, and more dependent on sufficient levels, although moisture limitation affects bryophyte activity (Rousk *et al.*, 2014, 2018). Interestingly, the bryophytes were not directly limited by light, but a low light saturation point could have contributed to this (Harley *et al.*, 1989; Marschall & Proctor, 2004; Wang *et al.*, 2016).

Bryophyte photosynthesis (III), in other words, gives ample opportunity for bryophyte-associated N₂-fixation (II). Furthermore, the results of Papers II and III showed that bryophytes are active outside of the summer season (July–August)—in fact, several species thrive more outside of summer than during the summer where they might suffer from drought. With large seasonal variations in environmental conditions, bryophyte-associated N₂-fixation and bryophyte photosynthesis were found to have adapted to these adverse conditions.

Plant relative ^{15}N tracer recovery

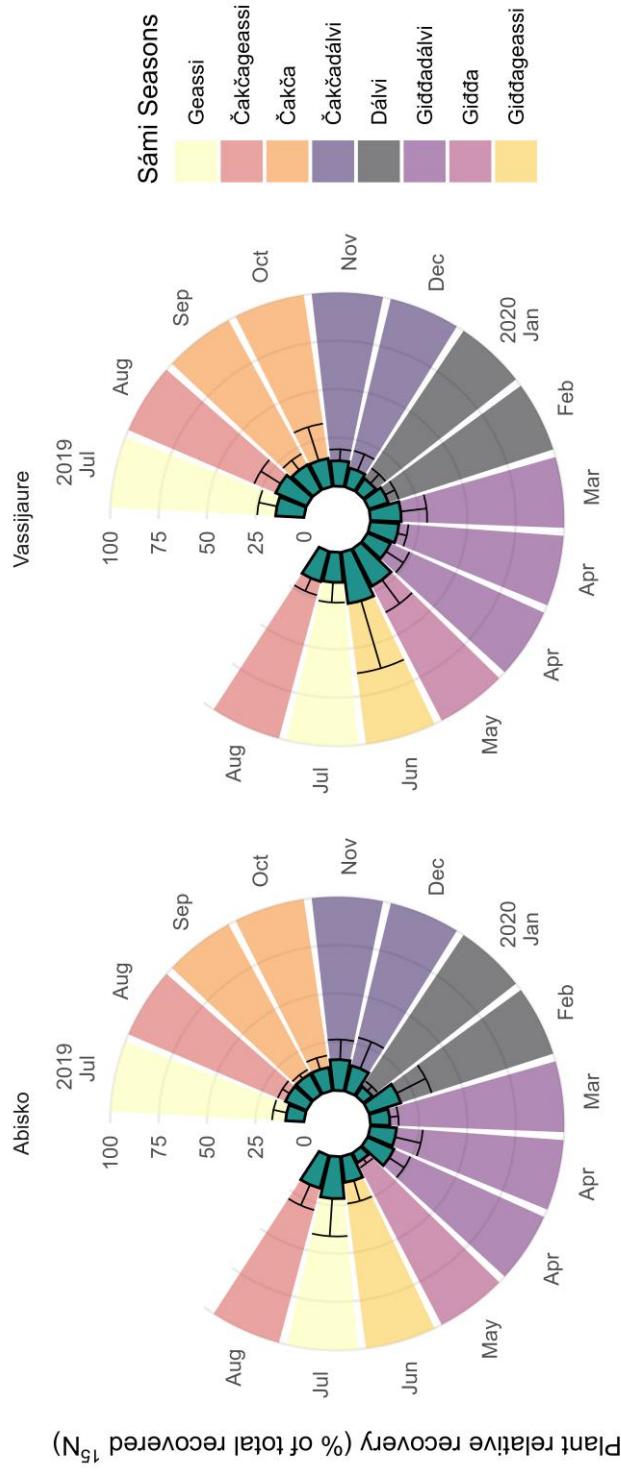


Figure 6 Plant recovery (%) of ^{15}N label relative to total ecosystem recovery (set at 100%). Sampling was done every 4 weeks from July 2019 to August 2020, as such there are two April measurements. The monthly bars are from when the experimental plots were harvested but represent estimated uptake over a three-week period between labelling and harvest. Error bars represent 95% confidence intervals ($n = 5$). The seasonal colours correspond to the eight seasons of the Northern latitudes.

Bryophyte ethylene production

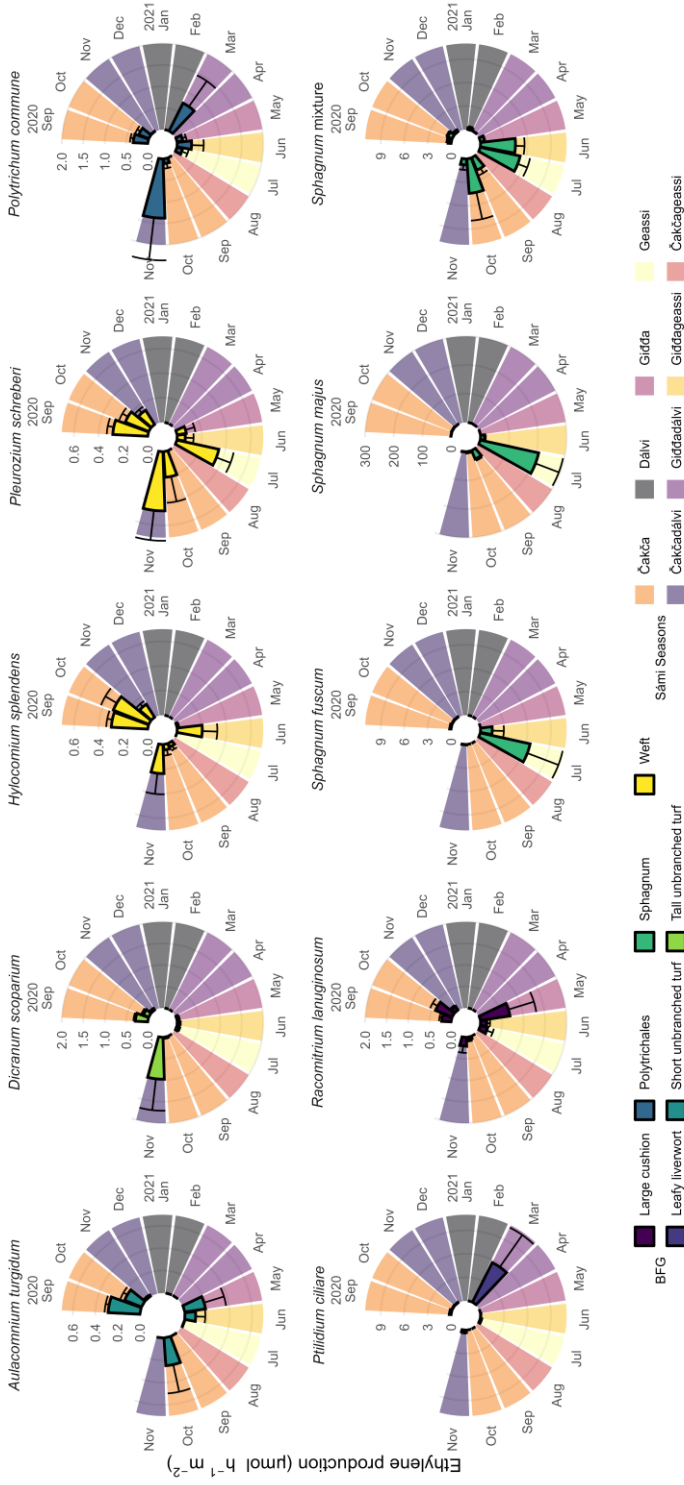


Figure 7 Bryophyte N_2 -fixation as measured with acetylene reduction assay (ethylene production). Measurements are from chamber-based field measurements during the period September 2020 to November 2021—note that not every month was measured. Values are mean ($n = 5$) for each transplanted bryophyte species. The BFG is bryophyte functional groups (Lett et al., 2022). Notice that the y-axes are different between species. The error bar is standard error. The seasonal colours correspond to the eight seasons of the Northern latitudes.

Bryophyte gross primary production

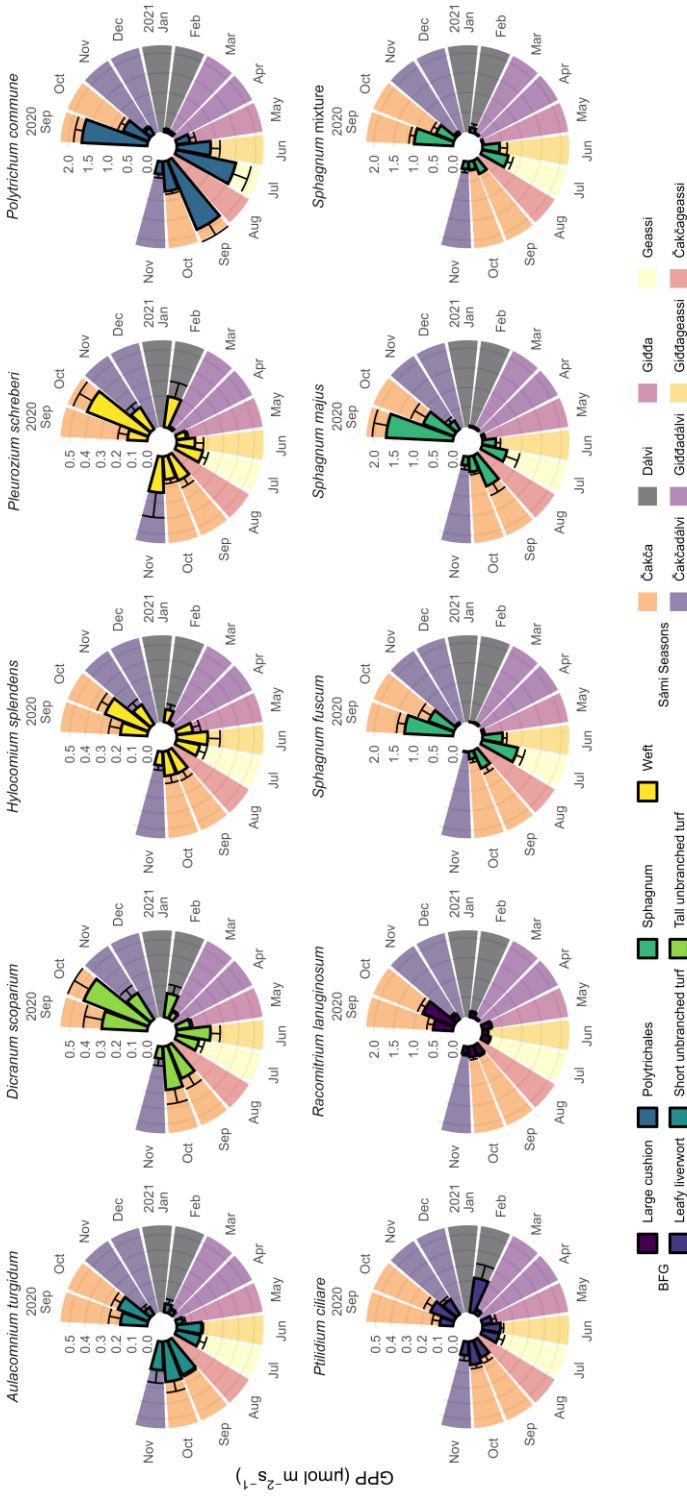


Figure 8 Bryophyte gross primary production (GPP) as positive CO_2 uptake. Measurements are from field measurements during the period September 2020 to November 2021—note that not every month was measured. Values are mean ($n = 5$) for each transplanted bryophyte species. The BFG is bryophyte functional groups (Lett et al., 2022). Notice that the y-axes are different between species. The error bars is standard error. The seasonal colours correspond to the eight seasons of the Northern latitudes.

Concluding remarks

Vascular plants are able to take up N throughout the year in a high-latitude, low-arctic ecosystem (I). While this might be dependent on environmental conditions, such as sufficient snow cover early on to stabilize soil temperatures at relatively high levels, there clearly will be years where it is possible for plants to stay active belowground during cold season months. This might boost their growth the following summer. The continued nutrient uptake also suggests that there is a temporal mismatch between energy (C) capture over summer and nutrient acquisition during the whole year. Paper I also emphasises the importance of considering plant belowground activity when aiming to understand the seasonal processes of vascular plants.

Bryophytes, in a similar low-arctic ecosystem, have strong seasonal patterns in their N₂-fixation (II) and photosynthetic activity (III); with high photosynthesis and N₂-fixation in the shoulder seasons and into the early- and late-winter. N₂-fixation, being a costly process (Turetsky, 2003), is regulated by energy supply. Given the continuous photosynthesis of the bryophytes of this study (III), it does not come as a surprise that bryophyte-associated N₂-fixation (II) can continue during most of the year, with some limitations in the middle of winter (*Dálvi*) and in the summer months when water limits both photosynthesis and N₂-fixation. Only *Sphagnum* species were able to fully utilize the summer for both photosynthesis and N₂-fixation, as they were not limited by moisture. Other factors also limit N₂-fixation, but it would be reasonable to assume that the primary limitation is not inactivity in the bryophytes nor a lack of available energy from photosynthetic activity. Furthermore, these patterns were found across a range of different bryophyte functional groups, suggesting that while there are species differences, bryophytes are overall active outside of summer.

Overall both vascular plants and bryophytes maintain activity for a much longer part of the year than has previously been presumed. The period from which they can acquire nutrients and energy goes beyond what is the traditional growing season from snowmelt until aboveground senescence. Instead, there are clear seasonal aspects that will need to be considered to understand plant growth and activity in high-latitude ecosystems. The cold season is not a “dormant” winter, and the perception of completely dormant plants, while incorrect today, will potentially be

even less so in the future with a changing climate (IPCC, 2021). If we are to fully understand how plants behave today, how changing climate will affect them, and what these processes mean on a larger global scale, we need to consider plant activity in the “omitted seasons” of the high latitudes.

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To family and friends, I send my thanks to you all for your support! Somehow I made it here.

My pleasure in fieldwork has not been reduced by the enormous amount of field- and lab work that was involved in these projects (and the unnamed 4th project that has not yet been completed). I leave the introduction and summary of my work with this Taoist story from Chuang Tzu (c. 300 BC), for no apparent reason, and with no further meaning behind it, unless, of course, you choose to find meaning in it.

When Chuang Tzu was angling in the river P'u, the king of Ch'u sent two high officers of state, who accosting Chuang Tzu announced that the king wished to entrust him with the management of all his domains. Rod in hand and eyes still fixed upon his line, Chuang Tzu replied, 'I have been told that in Ch'u there is a holy tortoise that died three thousand years ago. The king keeps it in the great hall of his ancestral shrine, in a casket covered with a cloth. Suppose that when this tortoise was caught, it had been allowed to choose between dying and having its bones venerated for centuries to come or going on living with its tail dragging in the mud, which would it have preferred?' 'No doubt,' said the two officers, 'it would have preferred to go on living with its tail dragging in the mud.'

'Well then, be off with you,' said Chuang Tzu, 'and leave me to drag my tail in the mud.'

— *Chuang Tzu* translated by Arthur Waley —